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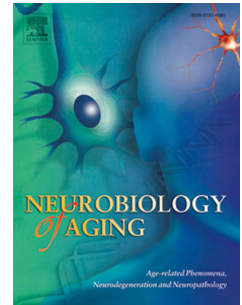
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Bridging the brain structure – brain function gap in prosodic speech processing in older adults

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Abstract

Age-related decline in speech perception may result in difficulties partaking in spoken conversation and potentially lead to social isolation and cognitive decline in older adults. It is therefore important to better understand how age-related differences in neurostructural factors such as cortical thickness (CT) and surface area (CSA) are related to neurophysiological sensitivity to speech cues in younger and older adults.

Age-related differences in CT and CSA of bilateral auditory-related areas were extracted using FreeSurfer in younger and older adults with normal peripheral hearing. Behavioral and neurophysiological sensitivity to prosodic speech cues (word stress and fundamental frequency of oscillation) were evaluated using discrimination tasks and a passive oddball paradigm, while EEG was recorded, to quantify mismatch negativity (MMN) responses.

Results revealed (a) higher neural sensitivity to word stress in older adults compared to younger adults, suggesting a higher importance of prosodic speech cues in the speech processing of older adults and (b) lower CT in auditory-related regions in older compared to younger individuals, suggesting neuronal loss associated with aging. Within the older age group, less neuronal loss (i.e. higher CT) in a right auditory-related area (i.e. the supratemporal sulcus) was related to better performance in fundamental frequency discrimination, while higher CSA in left auditory-related areas was associated with higher neural sensitivity towards prosodic speech cues as evident in the MMN patterns. Overall, our results offer evidence for neurostructural changes in aging that are associated with differences in the extent to which left and right auditory-related areas are involved in speech processing in older adults. We argue that exploring age-related differences in brain structure and function associated with decline in speech perception in older adults may help develop much needed rehabilitation strategies for older adults with central age-related hearing loss.

Words: 288

Key Words: prosody perception, aging, central hearing loss, auditory atrophy, cortical thickness, cortical surface area, mismatch negativity, AST hypothesis, lateralization, dedifferentiation

1. Introduction

A majority of older adults who have age-related hearing loss show deficient speech perception, in particular poorer performance in speech perception in noise (Helfer and Wilber, 1990; Zekveld et al., 2011), in speech perception in babble noise (Dubno et al., 1984), in fricative discrimination (Giroud et al., 2017) as well as in perception of time compressed speech (Gordon-Salant and Fitzgibbons, 2001) as compared to individuals with normal-for-age hearing. Because of the difficulty to understand speech, age-related hearing loss may therefore reduce the frequency that older adults partake in spoken conversations as well as the quality thereof (Heinrich et al., 2015; Vannson et al., 2015). Indeed, difficulties in engaging in spoken communication have been shown to cause social isolation, higher rates of depressive symptoms as well as lower quality of life and increased risk of dementia (Arlinger, 2003; Heinrich et al., 2015; Lin et al., 2011; Vannson et al., 2015). Hence, age-related hearing loss is considered one of the top three leading causes of disability in older adults (Mathers et al., 2008) and affects approximately 30% of older adults at the age of 65 years and older (Homans et al., 2017) and approximately 50% of older adults above the age of 80 years (Roth et al., 2011).

Meanwhile, it has been reported that older adults **without clinically disabling hearing loss** also show lower speech perception performance in various tasks as compared to younger adults, for example in speech in noise tasks (Giroud et al., 2018a; Goossens et al., 2017; Helfer and Wilber, 1990), in speech in babble noise tasks (Dubno et al., 1984), in time compressed speech perception tasks (Gordon-Salant and Fitzgibbons, 1993), in gap detection tasks (Harris et al., 2010), in temporal order discrimination tasks (Fogerty et al., 2010, 2012), in temporal fine structure processing (Lorenzi et al., 2006), as well as in fricative discrimination tasks (Giroud et al., 2018b). **Thus, deficient speech perception may not only be caused by age-related hearing loss due to a decline in inner ear functions (i.e., peripheral age-related hearing loss)** and is usually measured by audibility thresholds in the audiogram (Pickles, 2012). It is rather accompanied, complemented or even reinforced by central age-related hearing loss (Humes et al., 2012). Central age-related hearing loss occurs as a function of age-related atrophy in auditory brain circuits (Giroud et al., 2018a; Profant et al., 2014) occasionally following auditory deafferentation after damage to the cochlear periphery (Lin et al., 2014; Peelle and Wingfield, 2016)

or cognitive decline (Humes et al., 2012; Rosemann and Thiel, 2018) and may lead to speech perception difficulties in older individuals independently of elevated audibility thresholds in the audiogram (Giroud et al., 2018a). In other words, a considerable number of older individuals who are classified as "normal hearing" suffer in fact from an impairment of the central auditory system that severely affects speech perception.

Even though most of the research which compares older adults with age-appropriate peripheral hearing to younger adults suggests that older adults perform worse in speech perception, it has also been shown that older adults may benefit from prosodic speech cues, here defined as slowly changing suprasegmental modulations of spectral speech information (Meyer et al., 2018), to a similar extent or even more as younger adults (Wingfield et al., 1992, 2000). For example, sentence recall has been shown to be better when prosodic cues are presented in line with the syntactic structure as compared to when syntax and prosody are placed in conflict, and this effect has been demonstrated to be larger in peripherally normal hearing older compared to younger adults (Wingfield et al., 1992). Furthermore, recognition of words devoid of segmental information has been shown to be facilitated to the same degree in younger and older adults when prosodic cues indicated the number of syllables and syllabic stress (Wingfield et al., 2000). Electrophysiological data have further revealed that older adults integrate sentence-level prosodic information in real-time during the resolving of early and late closure ambiguities (Steinhauer et al., 2010). In sum, converging evidence so far suggests that even though peripherally normal hearing older adults show considerable age-related decline in various speech perception tasks probably caused by central deficits, they more strongly make use of prosodic information available in spoken language and use word stress to facilitate speech perception to the same extent as younger adults.

Prosodic speech processing has repeatedly been associated with the integrity of right auditory-related areas in younger adults (Geiser et al., 2008; Hirschler et al., 2013; Liem et al., 2014; Meyer et al., 2002, 2004; Meyer, 2008). Moreover, studies investigating neural correlates of suprasegmental speech processing have often been embedded within the 'asymmetric sampling in time' (AST) framework

(Poeppel, 2003; Shalom and Poeppel, 2008). As predicted by the AST hypothesis, these studies found that slowly changing acoustic speech information unfolding in a longer timescale of about ~250 ms, such as prosody (Meyer, 2008; Rufener et al., 2016; Zatorre and Gandour, 2008), is preferentially processed by the right non-primary auditory-related areas, while rapidly changing information in the temporal fine-structure present in a shorter timescale of about ~25 ms, such as the more steady-state spectral characteristics of segments, is preferentially processed by the left non-primary auditory-related areas (Abrams et al., 2008; Doelling et al., 2014; Giraud and Poeppel, 2012; Gross et al., 2013; Hirschler et al., 2013; Liem et al., 2014; Luo and Poeppel, 2007, 2012; Peelle and Davis, 2012; Pena et al., 2012; Rufener et al., 2016). It has been proposed that this functional lateralization relates to a lateralization of intrinsic oscillatory processes sampling the incoming acoustic signal at different rates (Giraud and Poeppel, 2012). Rapid γ oscillations (~40 Hz) in the left auditory-related areas have been shown to entrain to the temporal fine structure of a speech signal, while slower θ oscillations (~ 3-7 Hz) have been shown to entrain to slowly changing suprasegmental cues in right auditory-related areas (Giraud and Poeppel, 2012). This functional lateralization of θ and γ oscillations in auditory-related areas has also been related to the higher density of large pyramidal cells (Hutsler and Galuske, 2003) and more myelination (Penhune et al., 1996) in the left auditory-related areas compared to the right auditory-related areas, which allows them to produce more γ bursts. In summary, the AST framework indicates that the processing of temporal fine structure is preferentially processed in the left auditory-related areas, while slowly changing speech cues are preferentially driven-by the right auditory-related areas in young adults.

Nevertheless, **only a few** studies have investigated lateralization involved in speech processing in aging populations. Yet, in one of our previous studies we observed that older adults who showed less age-related atrophy (i.e. higher cortical thickness) in the right Heschl's sulcus (HS) performed better in a speech perception in noise task, while there was no correlation with left auditory-related areas (Giroud et al., 2018a). Furthermore, older individuals who had less age-related atrophy (i.e. higher **cortical thickness, CT**) in the right supratemporal sulcus (STS) showed stronger rightward lateralization of θ oscillations during resting state, while there was no correlation between θ

lateralization and CT in left auditory-related areas (Giroud et al., 2018a). Thus, those results could be indicative of a stronger involvement of the right auditory areas in speech processing in older adults. This hypothesis is in line with a previous study which demonstrated that older individuals recruited right auditory-related areas in addition to left auditory-related areas during syllable discrimination, as was evident in their scalp EEG, whereas the younger group only recruited left auditory-related areas (Bellis et al., 2000). Furthermore, the observed stronger θ lateralization in older adults who had less auditory atrophy in our previous study (Giroud et al., 2018a) may reflect the higher sensitivity to slowly changing speech cues such as sentence intonation or word prosody. Taking these studies into account, we therefore hypothesize that the stronger involvement of the right auditory-related areas for speech perception in older adults may be tied to the higher sensitivity to prosodic speech cues observed in older adults. However, none of the previous studies assessed the sensitivity to prosodic speech cues directly, which means that evidence for a direct link between brain structure in right auditory-related areas and prosody perception in older adults is still missing.

In order to fill this research gap, we designed a study that applied a prosody perception paradigm, namely a word stress discrimination task in order to assess the sensitivity to prosodic cues in older adults and younger controls with age-appropriate peripheral hearing. Crucially, sensitivity to acoustic cues does not always directly translate into behavior (Steinhauer et al., 2010) which is why we used more neurophysiological fine-grained indicators of auditory sensitivity to word stress than merely discrimination performance. We therefore recorded neurophysiological mismatch negativity (MMN) responses to study neurofunctional sensitivity to word stress using a passive oddball paradigm. During the MMN recording we presented the German word /Hubschrauber/ (engl. helicopter), which has an inherent stress on the first syllable, and systematically moved the stress position to the second and third syllable while recording the MMN time-locked to each syllable. We expected an MMN to occur time-locked to the syllables where an acoustic difference between the standard stimulus and the deviant stimulus occurred (see Table 1 for detailed hypotheses). To the best of our knowledge, this is the first study to investigate age-related differences in word stress perception combining behavior, EEG, and morphological measures.

To quantify atrophy in auditory-related brain regions, we collected T1-weighted MRI images from all participants and analyzed the neuroanatomical patterns in six bilateral auditory regions using surface-based morphometry. In addition, in order to elucidate the relation between behavioral and neurofunctional measurements of word stress perception and age-related central hearing loss, we assessed indirect indicators of central age-related hearing loss, namely cortical thickness (CT) and cortical surface area (CSA). The investigation of CT and CSA separately allows us to disentangle differential aspects of cortical structure as CT and CSA have been described to have no genetic relationship (Rakic, 1988, 1995, 2007) and are considered to be independent (Meyer et al., 2014). To date, it appears that mainly CT is subject to plasticity and changes as a function of training, experience, and age (Bermudez et al., 2009; Engvig et al., 2010; Hurtz et al., 2014; see Meyer et al., 2016 for a more comprehensive discussion of this issue; Thambisetty et al., 2010). In other words, age-related central hearing loss which has manifested in auditory-related areas of the brain is most likely expected to be driven by a decline in CT, while CSA of predominantly left perisylvian areas is hypothesized to be more strongly intertwined with genetically determined characteristics of auditory perception and language comprehension (Giroud et al., 2018a; Meyer et al., 2014; Pontious et al., 2008).

In sum, we combined behavioral, neurofunctional and neurostructural data to investigate age-related differences in prosody perception, namely word stress perception, between younger and older adults without peripheral hearing loss. For the MMN word stress experiment, we expected to find a larger MMN to a stress on the third syllable compared to the second syllable as a function of top-down control as this is less common in German than a stress on the second syllable in three-syllabic words (Janssen, 2013; Jessen et al., 1995). Also, assuming that older adults would be sensitive to word stress to the same extent as younger adults, we expected them to evoke similar MMN magnitudes. Moreover, we expected to find a correlation between CT in right auditory-related areas and MMN magnitudes revealing that older individuals with less atrophy in these areas evoked stronger MMN responses signalling a higher sensitivity to prosodic cues.

2. Materials and Methods

2.1. Participants

In this study, 23 healthy older adults (OA) (age range = 67-84 years, $M_{age} = 72.39$ years, 11 females) and 15 younger controls (YA) (age range = 20-29 years, $M_{age} = 24.33$ years, 12 females) were included. All older participants scored above 26 points in the Mini-Mental State Examination (MMSE) (Folstein et al., 1975). Furthermore, participants reported that there was no past or present neurological, psychiatric, or ear disease. Also, no ear or brain surgery had ever been performed. Furthermore, they denied suffering from any language or hearing disorder such as tinnitus, sensorineural hearing loss or dyslexia. In addition, all participants were native speakers of (Swiss-) German, right-handed as assessed by the Annett Hand Preference Questionnaire (Annett, 1970), did not practice more than six hours of music per week, and were not bilingual in terms of that they had not learnt a second language in preschool age. All participants passed the safety requirements for MRI scanning in order to obtain a T1-weighted MR image, which was recorded for a previous study (Giroud et al., 2018a).

Only participants with age adequate peripheral hearing were included in this study. According to the World Health Organization (WHO) a pure-tone average (PTA) of 25 dB or less for frequencies 500, 1000, 2000, and 4000 Hz is graded as “no impairment”, while a PTA between 26 and 40 dB is rated as a “slight impairment” in the hearing impairment grading scale. Correspondingly, in this study we only included older adults with a PTA smaller than 30 dB to ensure that the stimulus material would be audible for each participant and that the PTA would not imply a peripheral hearing loss that could be diagnosed in a clinic. Furthermore, only participants with symmetrical hearing (no more than 15 dB difference between left and right ear) were included in this study. PTA was assessed using a probe-detection paradigm with pure tones presented for 16 ms and 250 ms at 500, 1000, 2000, and 4000 Hz, while the audibility thresholds (in dB) were averaged across all trials. Even though we used a conservative inclusion criterion for the peripheral hearing, there was a significant difference between

the two age groups in the PTA ($t(37)=-1.71$, $p=.048$, 1-tailed). The audiograms of the YA and the OA group of this study are depicted in Figure 1.

- - - Insert Figure 1 about here - - -

The local ethics committee of the Canton Zurich approved the study, and written informed consent was obtained from all participants. Participants were paid for their participation.

2.2. Stimulus material

The German word /Hubschrauber/ (English: helicopter) was recorded at a sampling rate of 44.1 kHz by a professional female speaker at the Phonetics Laboratory of the University of Zurich. The speaker was instructed to produce three versions of the word /Hubschrauber/, one with a stress on the first syllable, one with a stress on the second syllable and one with a stress on the last syllable. The realization of syllable stress involved a manipulation of the fundamental frequency of oscillation (f_0), which has been shown to be a relevant cue to mark stress in the German language (Jessen et al., 1995). Word stress is most common on the initial syllable in German (Jessen et al., 1995). For each of the three syllables of the word /Hubschrauber/, a stressed and an unstressed version was then segmented for subsequent stimulus manipulation. This was performed using Praat software (version 5.3.68, available here: <http://www.fon.hum.uva.nl/praat/>). All of the segmented files were first normalized to 72 dB and the duration was equalized between similar syllables. Furthermore, in order to create a stressed and an unstressed version of each syllable of the word /Hubschrauber/, which only differed in the f_0 contour while all other parameters (duration, amplitude, frequencies) were kept constant, the stressed f_0 contour was extracted for each syllable. Subsequently, for each unstressed syllable a version was created in which the extracted stressed syllable contour replaced the unstressed contour. This procedure resulted in 6 syllables, an unstressed and a stressed version of each of the three syllables of the word /Hubschrauber/ in which all other parameters except the f_0 contour were kept constant. Then, all the syllables were combined into three versions of the word /Hubschrauber/ (see Table 1 and Figure 2): First, one version consisted of the word with a stress on the first syllable, but no stress on the

second and third syllables. This stimulus was used as the standard stimulus in the mismatch negativity experiment because it exemplifies the typical German pronunciation of the word /Hubschrauber/. Second, a version with a stress on the second syllable, but no stress on the first or third syllables was used as Deviant 1 in the mismatch negativity experiment. Third, the version with a stress on the third syllable, but no stress on the first or second syllable was used as Deviant 2 in the mismatch negativity experiment. In addition, for the behavioral task only, for each of these three stimuli three other versions were created in which the f_0 on the stressed syllable was raised by 20 Hz, 30 Hz, and 40 Hz.

--- Insert Table 1 about here ---

--- Insert Figure 2 about here ---

2.3. Brain Function: Mismatch negativity

We used a standard passive oddball procedure to evoke the mismatch negativity (MMN) (Näätänen et al., 2007). Participants were seated in a comfortable chair at a distance of about 1 m in front of a screen, which played a silent movie without arousing content. Participants were instructed not to pay attention to the auditory stimuli. Presentation software (www.neurobs.com; version 14.9) controlled the experiment and presented the stimulus material at 72 dB SPL via in-ear headphones (Sennheiser CX271). The standard stimulus was presented 488 times ($p=0.75$), while each of the two deviant stimuli was presented 81 times (each $p=0.125$) in a randomized order with a jittered inter-stimulus interval of 1000 ms. EEG was continuously recorded using a 128-electrode system (BioSemi AcitveTwo, Amsterdam, the Netherlands) with a sampling rate of 512 Hz, online references CMS/DRL, and with online bandpass filter between 0.1-100 Hz. Impedances were kept below 30 k Ω . Brain Vision Analyzer Software (Version 2.1.0, Brainproducts, Munich, Germany) was used for preprocessing the data. The data was offline bandpass filtered between 0.1 - 80 Hz using a notch filter. Next, an independent component (ICA) analysis was applied to remove artifacts of eye movements (Jung et al., 2000). Noisy channels were interpolated (Perrin et al., 1987) using topographic interpolation (order: 4, degree: 10, lambda: 1E-05) and movement artifacts were removed with a semi-automatic raw data inspection (maximal voltage step 50 μ V/ms, maximal difference in 200 ms

intervals of 200 μ V). The data was then re-referenced to linked left and right mastoid and a narrower bandpass filter from 0.1-20 Hz (12dB/oct) was applied. Furthermore, the data was segmented into - 200 to 2000 ms segments time-locked to stimulus onset and baseline corrected with regard to the pre-stimulus interval (see Figure 3). For each participant, the segments consisting of the neural responses to the standard stimuli, the Deviant 1 stimuli and the Deviant 2 stimuli were then averaged, respectively. Additionally, in order to perform peak amplitude detection, the MMNs were extracted time-locked with -100 to 600ms with respect to each syllable and baseline corrected for the 100ms pre-syllable interval. This baseline correction for the signal time-locked to each syllable was crucial, as we expected to find differences within these baseline intervals between subjects as a result of the MMNs occurring in these time intervals which might influence the subsequent MMNs. For electrode Cz, amplitude peak detection was applied for the global negative maxima time-locked to Syllable 1 within 200 to 400 ms after stimulus onset (Syllable 1), time-locked to Syllable 2 within 100 to 300 ms (Syllable 2), and time-locked to Syllable 3 within 100 to 300 ms (Syllable 3) after syllable onset. The amplitude in an interval of \pm 10 ms around the peak was exported with respective peak latency for each participant separately for each MMN resulting in nine peak amplitudes and respective latencies for each participant. These were for the standard stimulus, the Deviant 1 and the Deviant 2 for each syllable (Syllable 1, Syllable 2, and Syllable 3), respectively.

2.4. Behavior: Word stress perception

After having performed the passive MMN experiment, participants completed an explicit behavioral word stress discrimination task so that we could evaluate the discrimination accuracy of the stimulus material used in the MMN experiment. It was not possible to collect behavioral data from 1 YA and 4 OAs due to technical reasons. Participants were instructed to press a button in a forced choice experiment and indicate whether a pair of words were the same or different by clicking the left mouse button for the same and the right mouse button if the two words were perceived to be different. We used two types of word pairs for this task. In the first, all possible combinations of word pairs consisting of the same three stimuli used for the MMN experiment were presented to the participants. In the second type of word pairs, two similar stimuli from the MMN experiment were paired, while

either the first or the second word was different in its pitch variant with a frequency shift of the stressed syllable of 20, 30, or 40 Hz. In total, 72 trials were randomly presented consisting of 36 trials with **identical stimuli** in a pair and 36 trials with different stimuli in a pair. The interval between the two words of a word pair was set to 200 ms, while the next trial started 700 ms after the participant's answer was registered. We compared discrimination accuracy between the two age groups for word pairs with a difference in stress position, or a difference of 20 Hz, 30 Hz, or 40 Hz in stress separately for each syllable of the word /Hubschrauber/.

2.5. Brain Structure: Cortical thickness and mean surface area

Two high resolution T1-weighted images were obtained for each participant from a 3.0 T Philips Ingenia scanner (Philips Medical Systems, Best, The Netherlands) with a 12-channel head-coil using an anatomical 3D Turbo-Field-Echo (TFE) sequence with echo time (TE) = 3.79 ms, repetition time (TR) = 8.18 ms, field of view (FOV) = 240 x 160 x 240 mm, acquisition matrix = 256 x 256, 160 slices per volume, and isotropic voxel size = 0.94 x 0.94 x 1 mm, flip angle (α) = 90°. For four older participants, only one T1-weighted image was acquired. In order to create a single image volume with high contrast-to-noise, the two obtained T1-weighted images were averaged for all other participants (Reuter et al., 2010).

FreeSurfer Image Analysis Suite (version 5.1.0.), which is documented online (<http://freесurfer.net/>), was used for cortical surface reconstruction. Several preprocessing steps for surface-based morphometry (SBM) as implemented in the established FreeSurfer pipeline were calculated in a fully automated way (Dale et al., 1999; Dale and Sereno, 1993; Fischl et al., 1999b, 1999a, 2001, 2002, 2004b, 2004a; Fischl and Dale, 2000; Reuter et al., 2010; Ségonne et al., 2004). In addition, the segmentation precision was manually checked in all participants leading to the exclusion of one older adult because of failed surface reconstruction. Subsequently, cortical surface area (CSA) and cortical thickness (CT), the minimal distance between gray-white matter border and the pial surface at each vertex (Fischl and Dale, 2000), were extracted at each vertex of the tessellated surface. CSA is specified as the mean surface area of the pial surface area and the gray-white matter surface area (**i.e., (pial surface area + gray-white matter surface area)/2**) of the region at the respective vertex. CT

has been validated using manual segmentation (Cardinale et al., 2014; Kuperberg et al., 2003; Salat et al., 2004) and histological analysis (Rosas et al., 2002). Additionally, it has been shown to be reliable in healthy older adults (Liem et al., 2015). CT and CSA of six bilateral ROIs, which have been shown to be involved in auditory perception and speech processing (Giroud et al., 2018a; Meyer et al., 2014) were extracted using the *aparc.a 2009s* annotation (Destrieux et al., 2010). These include the Planum Temporale (PT), Planum Polare (PP), Supratemporal Gyrus (STG), Supratemporal Sulcus (STS), Heschl's Gyrus (HG), Heschl's Sulcus (HS).

2.6. Statistical analyses

First, in order to statistically verify the occurrence of an MMN, we performed paired t-tests within each age group comparing the peak amplitude evoked by each of the two deviants to the peak amplitude evoked by the standard. Thus, we separately compared the peak amplitudes of Deviant 1 and Deviant 2 to the Standard which were extracted time-locked to the three syllables of the word /Hubschrauber/, respectively. Comparison to a baseline, in this case to the signal evoked by the standard stimulus, is crucial because of the consistently lower EEG power measured on the scalp in older adults (see Figure 3). We expected to find MMNs evoked by both deviants when the EEG signal was time-locked to Syllable 1, an MMN only evoked by Deviant 1 (but not Deviant 2) when the EEG was time-locked to Syllable 2, and an MMN only evoked by Deviant 2 (but not Deviant 1) when the EEG was time-locked to Syllable 3 (see hypotheses in Table 1). Notably, we defined the occurrence of an MMN as a statistically significant difference (uncorrected for multiple comparisons) in the peak amplitude between deviant and standard. In order to stay consistent in our statistical analysis pipeline, we performed the same paired t-tests for the latencies. Furthermore, to also statistically investigate age-related differences in the MMNs, we used univariate ANOVAs with the factor age group (YA, OA) correcting for PTA and gender (**i.e., PTA and gender were treated as covariates**) and compared the MMN magnitude (the difference of the peak amplitude between deviant and standard) between the two age groups in all conditions in which a significant MMN occurred in the two groups. Also, in order to compare the MMN magnitude between the different conditions in which a significant MMN

occurred, a repeated measures ANOVA correcting for PTA and gender was performed within each age group.

- - - Insert Figure 3 about here - - -

Second, the accuracy of the behavioral discrimination task was analyzed using a univariate ANOVA (YA, OA) correcting for PTA and gender to compare age-related differences in discrimination of the stimulus material used for the MMN experiment, which only differed in the stress position within the word /Hubschrauber/ (stress either on the first, second, or third syllable). In addition, we computed a repeated measures ANOVA correcting for PTA and gender using the factors syllable (Syllable 1, Syllable 2, Syllable 3), f_0 difference (20 Hz, 30 Hz, 40 Hz), and age group (YA, OA) in order to assess discrimination performance differences with respect to age group and f_0 differences within syllables.

Third, age group differences in CT and CSA of the six bilateral ROIs were examined using univariate ANOVAs controlled for PTA and gender which were corrected for multiple comparisons by applying Bonferroni correction (alpha error divided by the number of tests) leading to a lowering of the alpha level from $\alpha = .05$ to $\alpha = .0042$ for the 12 ROIs compared between the two age groups (Giroud et al., 2018a; Wong et al., 2010).

Fourth, in order to elucidate the relation between brain structure and brain function in the older adults, two-tailed partial correlations between MMN amplitudes and CT and CSA in the 12 ROIs were calculated using similar Bonferroni corrections as explained above, while also correcting for PTA and gender. Furthermore, similar partial correlations were calculated with CT and CSA in the 12 ROIs and the behavioral data.

3. Results

3.1. Age-related differences in the mismatch negativity evoked by word stress

Unexpectedly, we did not find an MMN time-locked to Syllable 1 in the YA, neither for Deviant 1 nor for Deviant 2 (Deviant 1: $t(14)=-.93$, $p=.370$, Deviant 2: $t(14)=1.76$, $p=.101$) (see Table 2 and Figure 4). However, in the OA, we found an MMN time-locked to Syllable 1 evoked only by the Deviant 1 (Deviant 1: $t(22)=2.13$, $p=.045$, Deviant 2: $t(22)=-.78$, $p=.443$). **Furthermore, as predicted, an MMN time-locked to Syllable 2 was evoked in both age groups by the Deviant 1 only** (YA: Deviant 1: $t(14)=2.33$, $p=.036$, Deviant 2: $t(14)=1.99$, $p=.066$; OA: Deviant 1: $t(22)=4.40$, $p<.001$, Deviant 2: $t(22)=1.66$, $p=.111$). Also, in the OA we found an MMN time-locked to Syllable 3 evoked by the Deviant 2 only, as predicted (Deviant 1: $t(22)=-.84$, $p=.408$, Deviant 2: $t(22)=2.44$, $p=.023$). However, we did not find any MMN in the YA when time-locked to Syllable 3 (Deviant 1: $t(14)=.31$, $p=.761$, Deviant 2: $t(14)=1.08$, $p=.298$). The age group comparison between the MMN time-locked to Syllable 2 evoked by Deviant 1 (which was the only one we found in both age groups) did not yield a significant difference between YA and OA ($F(1,34)=.73$, $p=.399$). Also, the three significant MMNs which we found in the OA group, did not differ in magnitude from each other ($F(2,40)=.85$, $p=.861$). The same analyses for the latency revealed that there were no significant differences between deviants and standard stimuli (all t 's < -1.66 , all p 's $> .119$), except for the signal time-locked to Syllable 3 evoked by Deviant 2 in the OA ($t(22)=2.30$, $p=.031$).

Overall, these findings show that our data are not in accordance with Hypothesis 1. Neither the YA, nor the OA evoked an MMN time-locked to Syllable 1 even though the deviants were slightly different from the standard stimulus in their f_0 (18 Hz). However, we could find evidence for Hypothesis 2 in the two age groups revealing that YA and OA processed an unexpected word stress on Syllable 2 (with a difference in f_0 to the standard stimulus of 73 Hz). Similarly, Hypothesis 3 was confirmed, and the analyses revealed that an unexpected word stress of 53.54 Hz on Syllable 3 was flagged by the auditory circuits. However, only the OA were sensitive to this difference, not the YA.

- - - Insert Figure 4 about here - - -

- - - Insert Table 2 about here - -

3.2. Age-related differences in behavioral word stress perception

The two age groups performed well in discriminating the three stimuli from the MMN experiment (YA: 91.67 % correct (SD: 9.60 %), OA: 86.55% correct (SD: 17.60 %)). We did not observe any statistically significant difference between the groups ($F(1,29)=.22, p=.64$). Furthermore, a repeated measures ANOVA was calculated to evaluate age group differences in discrimination performance between the MMN stimuli and the same stimuli shifted by 20, 30, and 40 Hz in their f_0 of the stressed syllable. The repeated measures ANOVA with the factors syllable (Syllable 1, Syllable 2, Syllable 3), f_0 difference (20 Hz, 30 Hz, 40 Hz), and age group (YA, OA) revealed a significant main effect of f_0 difference ($F(2,58)=4.97, p=.01, \eta^2_p=.15$) showing that the 20 Hz difference was the most difficult to perceive (49.10 % correct), while the 30 Hz difference was moderately difficult to perceive (68.13% correct), and the 40 Hz difference was the easiest to discriminate (78.62 % correct), all post hoc p 's < .025 (see Figure 5). Furthermore, there was a main effect of age group ($F(1,29)=18.59, p<.011, \eta^2_p=.39$) showing that the OA performed worse than the YA (YA: 83.56 % correct, OA: 47.01% correct) across all conditions **suggesting that, on average, the OAs performed on chance level (indicated also by the not significant t-test against the 50% chance level in the OAs: $t(18)=-.52, p=.61$)**. Furthermore, there was a significant interaction between syllable, f_0 difference and PTA ($F(4,116)=2.55, p=.043, \eta^2_p=.08$) suggesting that f_0 differences were most difficult to discriminate on Syllable 1, moderate on Syllable 2 and easier on Syllable 3 and that this was particularly true for the 20 Hz difference.

In order to make sure that there was no bias towards responding “same” or “different”, we furthermore calculated the false alarm rate for each age group for the task. There was no difference ($t(31)=-.63, p=.53$) between the YA and the OA in the false alarm rate and the false alarm rate was generally low (YA: M=5.95%, SD=5.65%; OA: M=7.89%, SD=10.32%).

Thus, these results suggest that the OA performed worse across all conditions even though the PTA differences between YA and OA were controlled for and all participants were classified as normal hearing. Furthermore, our results suggest that the 20 Hz word stress difference was too difficult to perceive for OA, especially on the first and second syllables. But also, for the YA, the 20 Hz

1 difference was the most difficult to discriminate, even though they performed better than OA.

2 Interestingly, across the two age groups, this 20 Hz difference was also most difficult to discriminate
3 when on the first syllable on which a word stress can be expected in the German language and on
4 which the word stress is correct for the word /Hubschrauber/.

5
6 - - - Insert Figure 5 about here - - -
7

8 3.3. Age-related differences in auditory cortical structure

9 Similar to our previous study (Giroud et al., 2018a), the older adults **showed** lower cortical thickness
10 in all six left and right auditory brain areas than the younger adults (see Table 3), but cortical surface
11 area measurements of similar size as in younger participant. This result points to the fact, that the older
12 adults in this sample experienced age-related atrophy in bilateral auditory brain regions which was
13 reflected by the lower CT in these brain regions.

14
15 - - - Insert Table 3 about here - - -
16

17 3.4. The relation between brain structure and brain function

18 In order to investigate the structure-function relationship in the OA group, partial correlations between
19 the extent of age-related auditory atrophy as measured by CT as well as CSA in the six bilateral
20 auditory brain regions and the peak amplitude of the MMN were calculated. Because we did not find
21 any significant differences between the magnitudes of the three MMNs which were significantly
22 evoked in the OA, we created an average MMN in order to reduce the number of correlations we
23 calculated. However, we did not find any significant correlations with the CT of the six bilateral
24 regions, but did find these with the CSA of the left STG and the left HS (after correcting for multiple
25 comparisons by applying a lowered α threshold of .0042 with $r = -.62$, $p = .003$ and $r = -.65$, $p = .002$,
26 respectively). Thus, older individuals with larger mean surface area in two left auditory-related areas
27 also evoked higher MMN amplitudes (see Figure 6).

Furthermore, we calculated similar partial correlations with brain structure and behavior in the OA group, specifically with the discrimination accuracy of the 20 Hz f_0 differences, because this was the behavioral condition in which age-related differences were the strongest. We found one positive significant correlation (after correction for multiple comparisons), namely with the cortical thickness of the right STS ($r=.69, p=.002$). Thus, in this difficult perceptual task, older adults who had thicker right STS performed better.

- - - Insert Figure 6 about here - - -

4. Discussion

The aim of the present study was to examine, for the first time, the relationship between auditory brain structure and word-level prosody perception in younger and older adults with peripherally normal hearing. By means of the surface-based morphometry approach, we were able to capture two independent structural measurements of auditory-related areas, namely CT and CSA, and their relations with functional (MMN) and behavioral parameters of word stress sensitivity. Using the MMN paradigm we were able to analyze word stress perception time-locked to different syllables of the same word with varying stress.

As predicted, we found that a stress difference on the last syllable in a German word was easier to detect behaviorally (for both groups) than a difference on the second syllable. It has been shown that a stress on the last syllable is very uncommon in the German language (Jessen et al., 1995) which may therefore result in higher sensitivity to acoustic changes on the last syllable yielding a better recognition of the anomaly. In principle, the MMN data reflect this behavioral result, but interestingly, in the older group only. Our data therefore suggest that the older individuals exhibit higher neural sensitivity towards f_0 differences in words than younger adults.

In other words, the MMN results show that the older adults were more sensitive to varying f_0 patterns in words than the younger adults, even though the two groups both discriminated the word stress

variations of the word /Hubschrauber/ with a high accuracy in the behavioral task. This finding suggests that the older adults' MMNs were more strongly driven by the acoustic differences in f_0 and therefore by the acoustic properties of the stimulus material (i.e. bottom-up). The acoustic sensitivity towards word stress patterns was therefore more robust in older than in younger individuals. Simultaneously, we assume that the younger adults did not evoke MMNs time-locked to Syllables 1 and 3 because this acoustic difference is irrelevant in the German language as word stress patterns do not mark linguistic properties relevant to understand a word. Despite this fact the young adults were able to acoustically differentiate the stressed and unstressed syllables as reflected in the behavioral data. Word stress patterns in the German language only rarely mark word meanings and are therefore not fundamental to the understanding of the meaning of a word (Janssen, 2013). The older adults therefore relied more on the acoustic information overall, while the younger adults' MMN responses were more strongly driven by their linguistic experience (i.e. top-down). Yet, the younger adults still evoked an MMN time-locked to Syllable 2. However, Syllable 2 had the most pronounced acoustic difference with 73 Hz between the stressed and unstressed version and therefore might have evoked a **strong** response in all participants regardless of its linguistic importance.

A study which supports our observations in bottom-up and top-down processing comes from the visual domain (Werkle-Bergner et al., 2009). In this study, older adults showed more γ phase-stability between trials evoked by small visual stimuli as compared to younger adults, suggesting higher temporal bottom-up stability in older adults which may be a result of cortical reorganization because of increased neuronal loss (Werkle-Bergner et al., 2009). Such higher neuronal loss has also been shown to trigger reorganizing effects in the auditory modality expressed in age-related differences in the extent of functional (Keller et al., 2019) and structural (Giroud et al., 2018a) involvement of left and right auditory-related areas in speech perception. In the current study, the lower CT in auditory-related areas in the older group may similarly reflect higher neuronal loss. Moreover, we have previously shown that such lower CT, specifically in right auditory-related areas, resulted in lower speech perception performance in supra-threshold frequency selectivity, supra-threshold temporal compression, speech in noise perception, as well as higher neural activity during tonal perception in

older adults (Giroud et al., 2018a; Profant et al., 2015). At the same time, these relations between speech perception and CT in right auditory-related structures were not present in younger adults (Giroud et al., 2018a). Similarly, higher white-matter integrity in the right superior longitudinal fasciculus and the right uncinate fasciculus has been shown to be associated with better hearing performance in older adults (Rigters et al., 2018). The results of the current study fit into this pattern revealing that older adults with less age-related atrophy (i.e. thicker) right STS performed better in the 20 Hz f_0 discrimination task ($R^2=.48$).

In sum, the interpretation of these results is twofold. First, as predicted, they suggest that age-related structural decline in auditory-related areas, signaling central age-related hearing loss, is associated with a reorganization in auditory lateralization, namely a stronger involvement of right auditory-related areas in speech perception. Second, cortical atrophy in right auditory-related areas explained 48% more variance than pure-tone thresholds in the f_0 discrimination task, highlighting the importance of considering central hearing loss, here defined as age-related structural decline in auditory-related areas as indicated by lower CT, when investigating speech perception in older adulthood. Since audiograms are not able to capture such age-related differences in auditory perception, we believe it is crucial to include such alternative measures to assess hearing loss in older adults.

Importantly, we did not find any relation between CT in auditory-related areas and the MMN evoked by word stress. However, there was also no age-related decline in word stress perception as indicated by the MMN results. Still, our analyses revealed a significant correlation between cortical surface area in the left STG and the left HS and the MMN in older adults. We interpret this finding as first evidence that older adults who have larger cortical surface area (Pontious et al., 2008) in left auditory brain regions, may to some degree be better able to cope with structural decline reflected by lower CT in that they may be better able to use sensory-driven prosodic cues in a speech signal. As argued by Meyer et al. (2014), larger CSAs in left auditory-related areas reflect more widely spaced neuronal columns which enables the recognition and storage of over-learned spectro-temporal acoustic patterns in an efficient and automatic manner. Thus, it is likely that a larger CSA in left auditory regions would

allow older adults' ability to perceive complex spectro-temporal patterns to be more robust as they progress into old age.

Furthermore, because this relation between CSA and sensitivity to prosodic speech cues in older adults existed only with the left auditory-related areas, contrary to our predictions, this result suggests that there are global age-related changes in auditory lateralization related to speech perception. As mentioned above, stronger involvement of the right auditory-related areas in speech perception has been shown in older adults (Giroud et al., 2018a; Keller et al., 2019) in a variety of speech perception tasks, while in younger adults findings typically point to stronger involvement of left auditory-related areas for speech perception in general, and stronger recruitment of right auditory-related areas in prosodic speech perception (Meyer et al., 2002, e.g. 2004). Overall, we therefore find that the less specialized hemisphere (i.e., the right auditory-related areas) is more strongly involved in speech perception in older adults, a cortical reorganization which may result from age-related neuronal loss. Furthermore, this suggests less specialization or differentiation in the auditory-related areas during speech perception in aging similar to results of a previous study using fMRI (Profant et al., 2015), a mechanism which has also been associated with aging in other domains (see Cabeza, 2002 for an overview). Thus, these results allow the AST model to expand, for the first time, into aging. As already suggested by Poeppel and colleagues in 2008, it is generally possible that the left auditory-related areas also entrain to slowly changing speech cues such as prosody (Poeppel et al., 2008). We therefore interpret that older adults involve the left auditory-related areas in addition to the right to counteract the structural decline of these areas (Keller et al., 2019), allowing high sensitivity to prosodic speech cues until old age.

In general, we can infer that the higher word stress sensitivity in older compared to younger adults which we found in the MMN experiment does not result from a generally higher sensitivity to f_0 because of the lower performance of the older adults in the behavioral f_0 discrimination task (discriminating 20, 30, and 40 Hz f_0 differences on the same syllable). Instead, we interpret this finding to indicate that older adults only show higher sensitivity to f_0 when f_0 is marking a syllable in a word

(as measured by the MMN experiment) compared to when f_0 indicates the strength of a syllable stress (as measured in the behavioral experiment). In that sense, syllable stress in a word has been shown to indicate the rhythm of a word, which may be an additional prosodic cue which older adults with difficulties to perceive the temporal fine structure of a word may use to maintain speech perception despite of proceeding atrophy.

For example, marked prosodic elements such as intonation and stress in speech, also called “elderspeak”, have been shown to be helpful for older adults to perceive speech and improve comprehension (Cohen and Faulkner, 1986). Similarly, older adults have been shown to be sensitive to prosodic speech cues to at least the same extent as younger adults (Wingfield et al., 1992, 2000). It is therefore conceivable that marked prosody such as in elderspeak may help older adults compensate for age-related decline in temporal fine structure processing. Word stress as a prosodic cue indicating the word rhythm may therefore be more important for older adults than for younger adults during speech perception, explaining the higher sensitivity in the MMN experiment towards word stress violations. However, it is important to keep in mind that not all types of prosodic marking have been shown to be helpful for older adults, because slowing the speech rate and using high f_0 have not been shown to improve understanding and can rather reflect aging stereotypes held by the speaker (Kemper and Harden, 1999).

The sensitivity for prosodic speech cues in older adults resembles some results from studies with infants. Assuming an extension of the AST predictions to infants, the stronger involvement of the right auditory-related areas during speech processing in 2-days old newborns (Perani et al., 2011) could be indicative of a high sensitivity to prosody. This is in line with research showing that 3-month old babies show right-lateralized hemodynamic responses during prosodic processing (Homae et al., 2006). While we wish to be cautious in the drawing of parallels between speech processing in infants and in older adults, the similar reliance on prosodic cues in the face of challenges to the understanding of speech (for infants: still learning the lexical cues of the specific language of their environment; for

older adults: difficulties processing the temporal fine structure such as phonemes) is worth noting in a study such as this one, in which the speech processing over the lifespan is in focus.

5. Conclusions

Our results suggest that older adults without clinically disabling peripheral HL show age-related structural differences (i.e. lower CT) in auditory-related areas that probably imply impaired speech perception beyond peripheral HL. Such age-related structural decline may lead to a neural reorganization in that the relative involvement of left and right auditory-related areas in speech perception becomes less differentiated across the lifespan. For example, we demonstrated that less structural decline (higher CSA) in left auditory-related areas is related to more sensitivity to prosodic speech cues in older adults, even though prosodic speech cues have been shown to be more strongly associated with right auditory-related areas in younger adults (Geiser et al., 2008; Hurschler et al., 2013; Liem et al., 2014). Furthermore, older adults were more sensitive to prosodic speech cues than younger adults indicating that prosodic speech cues such as word stress may be helpful for older adults who experience central age-related hearing loss.

Overall, investigating the extent to which older individuals use speech parameters such as prosody may reveal more insight into the reorganization of speech functions across the lifespan. Such research may inform the development of advanced training interventions for improving speech perception in older adults with normal audiograms to avoid the drastic consequences of untreated hearing loss. Such interventions could potentially include information on word stress and its relevance for understanding speech and/or auditory training improving the perception of prosodic cues in speech. Importantly, since most of the rehabilitation research targets older adults who have elevated audibility thresholds, many older adults who experience central age-related hearing loss and who have normal-for-age audiograms will not get professional help even though the severity of the consequences can be expected to be similar **to those** for individuals with peripheral hearing loss.

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References

- Abrams, D.A., Nicol, T., Zecker, S., Kraus, N., 2008. Right-Hemisphere Auditory Cortex Is Dominant for Coding Syllable Patterns in Speech. *J. Neurosci.* 28, 3958–3965. <https://doi.org/10.1523/JNEUROSCI.0187-08.2008>
- Annett, M., 1970. A classification of hand preference by association analysis. *Br. J. Psychol.* 61, 303–321.
- Arlinger, S., 2003. Negative consequences of uncorrected hearing loss—a review. *Int. J. Audiol.* 42, 17–20.
- Bellis, T.J., Nicol, T., Kraus, N., 2000. Aging affects hemispheric asymmetry in the neural representation of speech sounds. *J. Neurosci. Off. J. Soc. Neurosci.* 20, 791–797.
- Bermudez, P., Lerch, J.P., Evans, A.C., Zatorre, R.J., 2009. Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cereb. Cortex* N. Y. N 1991 19, 1583–1596. <https://doi.org/10.1093/cercor/bhn196>
- Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychol. Aging* 17, 85–100.
- Cardinale, F., Chinnici, G., Bramerio, M., Mai, R., Sartori, I., Cossu, M., Lo Russo, G., Castana, L., Colombo, N., Caborni, C., De Momi, E., Ferrigno, G., 2014. Validation of FreeSurfer-Estimated Brain Cortical Thickness: Comparison with Histologic Measurements. *Neuroinformatics* 12, 535–542.
- Cohen, G., Faulkner, D., 1986. Does “elderspeak” work? The effect of intonation and stress on comprehension and recall of spoken discourse in old age. *Lang. Commun.* 6, 91–98. [https://doi.org/10.1016/0271-5309\(86\)90008-X](https://doi.org/10.1016/0271-5309(86)90008-X)
- Dale, A.M., Fischl, B., Sereno, M.I., 1999. Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage* 9, 179–194. <https://doi.org/10.1006/nimg.1998.0395>
- Dale, A.M., Sereno, M.I., 1993. Improved Localization of Cortical Activity by Combining EEG and MEG with MRI Cortical Surface Reconstruction: A Linear Approach. *J. Cogn. Neurosci.* 5, 162–176. <https://doi.org/10.1162/jocn.1993.5.2.162>
- Destrieux, C., Fischl, B., Dale, A., Hagler, E., 2010. Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *NeuroImage* 53, 1–15. <https://doi.org/10.1016/j.neuroimage.2010.06.010>
- Doelling, K.B., Arnal, L.H., Ghitza, O., Poeppel, D., 2014. Acoustic landmarks drive delta–theta oscillations to enable speech comprehension by facilitating perceptual parsing. *NeuroImage* 85, 761–768. <https://doi.org/10.1016/j.neuroimage.2013.06.035>
- Dubno, J.R., Dirks, D.D., Morgan, D.E., 1984. Effects of age and mild hearing loss on speech recognition in noise. *J. Acoust. Soc. Am.* 76, 87–96. <https://doi.org/10.1121/1.391011>
- Engvig, A., Fjell, A.M., Westlye, L.T., Moberget, T., Sundseth, Ø., Larsen, V.A., Walhovd, K.B., 2010. Effects of memory training on cortical thickness in the elderly. *NeuroImage* 52, 1667–1676. <https://doi.org/10.1016/j.neuroimage.2010.05.041>
- Fischl, B., Dale, A.M., 2000. Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proc. Natl. Acad. Sci. U. S. A.* 97, 11050–11055. <https://doi.org/10.1073/pnas.200033797>
- Fischl, B., Liu, A., Dale, A.M., 2001. Automated manifold surgery: constructing geometrically accurate and topologically correct models of the human cerebral cortex. *IEEE Trans. Med. Imaging* 20, 70–80.
- Fischl, B., Salat, D.H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N., Rosen, B., Dale, A.M.,

2002. Whole brain segmentation: automated labeling of neuroanatomical structures in the human brain. *Neuron* 33, 341–355.
- Fischl, B., Salat, D.H., van der Kouwe, A.J.W., Makris, N., Segonne, F., Quinn, B.T., Dale, A.M., 2004a. Sequence-independent segmentation of magnetic resonance images. *NeuroImage* 23 Suppl 1, S69–84. <https://doi.org/10.1016/j.neuroimage.2004.07.016>
- Fischl, B., Sereno, M.I., Dale, A.M., 1999a. Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. *NeuroImage* 9, 195–207. <https://doi.org/10.1006/nimg.1998.0396>
- Fischl, B., Sereno, M.I., Tootell, R.B., Dale, A.M., 1999b. High-resolution intersubject averaging and a coordinate system for the cortical surface. *Hum. Brain Mapp.* 8, 272–284.
- Fischl, B., van der Kouwe, A., Destrieux, C., Halgren, E., Segonne, F., Salat, D.H., Busa, E., Seidman, L.J., Goldstein, J., Kennedy, D., Caviness, V., Makris, N., Rosen, B., Dale, A.M., 2004b. Automatically parcellating the human cerebral cortex. *Cereb. Cortex* 14, 11–22.
- Fogerty, D., Humes, L.E., Kewley-Port, D., 2010. Auditory temporal-order processing of vowel sequences by young and elderly listeners. *J. Acoust. Soc. Am.* 127, 2509–2520. <https://doi.org/10.1121/1.3316291>
- Fogerty, D., Kewley-Port, D., Humes, L.E., 2012. Asynchronous Vowel-Pair Identification Across the Adult Life Span for Monaural and Dichotic Presentations. *J. Speech Lang. Hear. Res.* 55, 487–499. [https://doi.org/10.1044/1092-4388\(2011/11-0102\)](https://doi.org/10.1044/1092-4388(2011/11-0102))
- Folstein, M.F., Folstein, S.E., McHugh, P.R., 1975. “Mini-mental state”: a practical method for grading the cognitive state of patients for the clinician. *J. Psychiatr. Res.* 12, 189–198.
- Geiser, E., Zaehle, T., Jancke, L., Meyer, M., 2008. The Neural Correlate of Speech Rhythm as Evidenced by Metrical Speech Processing. *J. Cogn. Neurosci.* 20, 541–552.
- Giraud, A.-L., Poeppel, D., 2012. Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci.* 15, 511–517.
- Giroud, N., Hirsiger, S., Muri, R., Kegel, A., Dillier, N., Meyer, M., 2018a. Neuroanatomical and resting state EEG power correlates of central hearing loss in older adults. *Brain Struct. Funct.* 223, 145–163. <https://doi.org/10.1007/s00429-017-1477-0>
- Giroud, N., Lemke, U., Reich, P., Bauer, J., Widmer, S., Meyer, M., 2018b. Are you surprised to hear this? Longitudinal spectral speech exposure in older compared to middle-aged normal hearing adults. *Eur. J. Neurosci.* 47, 58–68. <https://doi.org/10.1111/ejn.13772>
- Giroud, N., Lemke, U., Reich, P., Matthes, K.L., Meyer, M., 2017. The impact of hearing aids and age-related hearing loss on auditory plasticity across three months - An electrical neuroimaging study. *Hear. Res.* 353, 162–175. <https://doi.org/10.1016/j.heares.2017.06.012>
- Goossens, T., Vercammen, C., Wouters, J., van Wieringen, A., 2017. Masked speech perception across the adult lifespan: Impact of age and hearing impairment. *Hear. Res.* 344, 109–124. <https://doi.org/10.1016/j.heares.2016.11.004>
- Gordon-Salant, S., Fitzgibbons, P.J., 2001. Sources of age-related recognition difficulty for time-compressed speech. *J. Speech Lang. Hear. Res. JSLHR* 44, 709–719.
- Gordon-Salant, S., Fitzgibbons, P.J., 1993. Temporal factors and speech recognition performance in young and elderly listeners. *J. Speech Hear. Res.* 36, 1276–1285.
- Gross, J., Hoogenboom, N., Thut, G., Schyns, P., Panzeri, S., Belin, P., Garrod, S., 2013. Speech rhythms and multiplexed oscillatory sensory coding in the human brain. *PLoS Biol.* 11, e1001752.
- Harris, K.C., Eckert, M.A., Ahlstrom, J.B., Dubno, J.R., 2010. Age-related differences in gap detection: effects of task difficulty and cognitive ability. *Hear. Res.* 264, 21–29. <https://doi.org/10.1016/j.heares.2009.09.017>
- Heinrich, A., Henshaw, H., Ferguson, M.A., 2015. The relationship of speech intelligibility with hearing sensitivity, cognition, and perceived hearing difficulties varies for different speech perception tests. *Front. Psychol.* 6, 782. <https://doi.org/10.3389/fpsyg.2015.00782>
- Helfer, K.S., Wilber, L.A., 1990. Hearing loss, aging, and speech perception in reverberation and noise. *JSHR* 33, 149–155.
- Homae, F., Watanabe, H., Nakano, T., Asakawa, K., Taga, G., 2006. The right hemisphere of sleeping infant perceives sentential prosody. *Neurosci. Res.* 54, 276–280. <https://doi.org/10.1016/j.neures.2005.12.006>

- Homans, N.C., Metselaar, R.M., Dingemanse, J.G., Schroeff, M.P. van der, Brocaar, M.P., Wieringa, M.H., Jong, R.J.B. de, Hofman, A., Goedegebure, A., 2017. Prevalence of age-related hearing loss, including sex differences, in older adults in a large cohort study. *The Laryngoscope* 127, 725–730. <https://doi.org/10.1002/lary.26150>
- Humes, L.E., Dubno, J., Gordon-Salant, S., Lister, J., Cacace, A., Cruickshanks, K., Gates, G., Wilson, R., Wingfield, A., 2012. Central presbycusis: A review and evaluation of the evidence. *J. Am. Acad. Audiol.* 23, 635–666.
- Hurschler, M.A., Liem, F., Jäncke, L., Meyer, M., 2013. Right and left perisylvian cortex and left inferior frontal cortex mediate sentence-level rhyme detection in spoken language as revealed by sparse fMRI. *Hum. Brain Mapp.* 34, 3182–3192. <https://doi.org/10.1002/hbm.22134>
- Hurtz, S., Woo, E., Kebets, V., Green, A.E., Zoumalan, C., Wang, B., Ringman, J.M., Thompson, P.M., Apostolova, L.G., 2014. Age Effects on Cortical Thickness in Cognitively Normal Elderly Individuals. *Dement. Geriatr. Cogn. Disord. EXTRA* 4, 221–227. <https://doi.org/10.1159/000362872>
- Hutsler, J., Galuske, R.A.W., 2003. Hemispheric asymmetries in cerebral cortical networks. *Trends Neurosci.* 26, 429–435. [https://doi.org/10.1016/S0166-2236\(03\)00198-X](https://doi.org/10.1016/S0166-2236(03)00198-X)
- Janssen, U., 2013. UNTERSUCHUNGEN ZUM WORTAKZENT IM DEUTSCHEN UND NIEDERLÄNDISCHEN. Heinrich-Heine-Universität, Düsseldorf.
- Jessen, M., Marasek, K., Schneider, K., Clausen, K., 1995. Acoustic correlates of word stress and the tense/lax opposition in the vowel system of German, in: *Proceedings of the International Congress of Phonetic Sciences*. Stockholm University Stockholm, pp. 428–431.
- Jung, T.P., Makeig, S., Humphries, C., Lee, T.W., McKeown, M.J., Iragui, V., Sejnowski, T.J., 2000. Removing electroencephalographic artifacts by blind source separation. *Psychophysiology* 37, 163–178.
- Keller, M., Neuschwander, P., Meyer, M., 2019. When right becomes less right: Neural dedifferentiation during suprasegmental speech processing in the aging brain. *NeuroImage* 189, 886–895. <https://doi.org/10.1016/j.neuroimage.2019.01.050>
- Kemper, S., Harden, T., 1999. Experimentally disentangling what's beneficial about elderspeak from what's not. *Psychol. Aging* 14, 656–670. <https://doi.org/10.1037/0882-7974.14.4.656>
- Kuperberg, G.R., Broome, M.R., McGuire, P.K., David, A.S., Eddy, M., Ozawa, F., Goff, D., West, W.C., Williams, S.C., van der Kouwe, A.J., Salat, D.H., Dale, A.M., Fischl, B., 2003. Regionally localized thinning of the cerebral cortex in schizophrenia. *Arch. Gen. Psychiatry* 60, 878–888.
- Liem, F., Hurschler, M.A., Jäncke, L., Meyer, M., 2014. On the planum temporale lateralization in suprasegmental speech perception: Evidence from a study investigating behavior, structure, and function. *Hum. Brain Mapp.* 35, 1779–1789. <https://doi.org/10.1002/hbm.22291>
- Liem, F., Mérellat, S., Bezzola, L., Hirsiger, S., Philipp, M., Madhyastha, T., Jäncke, L., 2015. Reliability and statistical power analysis of cortical and subcortical FreeSurfer metrics in a large sample of healthy elderly. *NeuroImage* 108, 95–109. <https://doi.org/10.1016/j.neuroimage.2014.12.035>
- Lin, F.R., Ferrucci, L., An, Y., Goh, J.O., Doshi, J., Metter, E.J., Davatzikos, C., Kraut, M.A., Resnick, S.M., 2014. Association of hearing impairment with brain volume changes in older adults. *NeuroImage* 90, 84–92. <https://doi.org/10.1016/j.neuroimage.2013.12.059>
- Lin, F.R., Metter, E.J., O'Brien, R.J., Resnick, S.M., Zonderman, A.B., Ferrucci, L., 2011. Hearing loss and incident dementia. *Arch. Neurol.* 68, 214–220. <https://doi.org/10.1001/archneurol.2010.362>
- Lorenzi, C., Gilbert, G., Carn, H., Garnier, S., Moore, B.C.J., 2006. Speech perception problems of the hearing impaired reflect inability to use temporal fine structure. *Proc. Natl. Acad. Sci.* 103, 18866–18869. <https://doi.org/10.1073/pnas.0607364103>
- Luo, H., Poeppel, D., 2012. Cortical oscillations in auditory perception and speech: evidence for two temporal windows in human auditory cortex. *FPY* 3, 170.
- Luo, H., Poeppel, D., 2007. Phase patterns of neuronal responses reliably discriminate speech in human auditory cortex. *Neuron* 54, 1001–1010. <https://doi.org/10.1016/j.neuron.2007.06.004>
- Mathers, C., Fat, D.M., Boerma, J.T., World Health Organization (Eds.), 2008. The global burden of disease: 2004 update. World Health Organization, Geneva, Switzerland.

- 1 Meyer, M., 2008. Functions of the left and right posterior temporal lobes during segmental and
2 suprasegmental speech perception. *Z. Für Neuropsychol.* 19, 101–115.
3 <https://doi.org/10.1024/1016-264X.19.2.101>
- 4 Meyer, M., Alter, K., Friederici, A.D., Lohmann, G., von Cramon, D.Y., 2002. FMRI reveals brain
5 regions mediating slow prosodic modulations in spoken sentences. *Hum. Brain Mapp.* 17, 73–
6 88. <https://doi.org/10.1002/hbm.10042>
- 7 Meyer, M., Keller, M., Giroud, N., 2018. Suprasegmental Speech Prosody and the Human Brain, in:
8 Frühholz, S., Belin, P. (Eds.), *The Oxford Handbook of Voice Perception*. Oxford University
9 Press, Oxford.
- 10 Meyer, M., Liem, F., Hirsiger, S., Jäncke, L., Hänggi, J., 2014. Cortical surface area and cortical
11 thickness demonstrate differential structural asymmetry in auditory-related areas of the human
12 cortex. *Cereb. Cortex* 24, 2541–2552. <https://doi.org/10.1093/cercor/bht094>
- 13 Meyer, M., Neff, P., Liem, F., Kleinjung, T., Weidt, S., Langguth, B., Schecklmann, M., 2016.
14 Differential tinnitus-related neuroplastic alterations of cortical thickness and surface area.
15 *Hear. Res.* 342, 1–12. <https://doi.org/10.1016/j.heares.2016.08.016>
- 16 Meyer, M., Steinhauer, K., Alter, K., Friederici, A.D., Cramon, D.Y. von, 2004. Brain activity varies
17 with modulation of dynamic pitch variance in sentence melody. *Brain Lang.* 89, 277–289.
- 18 Näätänen, R., Paavilainen, P., Rinne, T., Alho, K., 2007. The mismatch negativity (MMN) in basic
19 research of central auditory processing: a review. *Clin. Neurophysiol.* 118, 2544–2590.
20 <https://doi.org/10.1016/j.clinph.2007.04.026>
- 21 Peelle, J.E., Davis, M.H., 2012. Neural Oscillations Carry Speech Rhythm through to Comprehension.
22 *Front. Psychol.* 3.
- 23 Peelle, J.E., Wingfield, A., 2016. The Neural Consequences of Age-Related Hearing Loss. *Trends*
24 *Neurosci.* 39, 486–497. <https://doi.org/10.1016/j.tins.2016.05.001>
- 25 Pena, M., Werker, J.F., Dehaene-Lambertz, G., 2012. Earlier speech Exposure does not accelerate
26 speech acquisition. *J. Neurosci.* 32, 11159–11163.
- 27 Penhune, V.B., Zatorre, R.J., MacDonald, J.D., Evans, A.C., 1996. Interhemispheric anatomical
28 differences in human primary auditory cortex: probabilistic mapping and volume
29 measurement from magnetic resonance scans. *Cereb. Cortex N. Y. N* 1991 6, 661–672.
- 30 Perani, D., Saccuman, M.C., Scifo, P., Anwander, A., Spada, D., Baldoli, C., Poloniato, A., Lohmann,
31 G., Friederici, A.D., 2011. Neural language networks at birth. *Proc. Natl. Acad. Sci.* 108,
32 16056–16061. <https://doi.org/10.1073/pnas.1102991108>
- 33 Perrin, F., Pernier, J., Bertrand, O., Giard, M.H., Echallier, J.F., 1987. Mapping of scalp potentials by
34 surface spline interpolation. *Electroencephalogr. Clin. Neurophysiol.* 66, 75–81.
- 35 Pickles, J.O., 2012. *An introduction to the physiology of hearing*, 4. ed. ed. Emerald, London.
- 36 Poeppel, D., 2003. The analysis of speech in different temporal integration windows: cerebral
37 lateralization as asymmetric sampling in time. *Speech Commun.* 41, 245–255.
- 38 Poeppel, D., Idsardi, W.J., van Wassenhove, V., 2008. Speech perception at the interface of
39 neurobiology and linguistics. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 363, 1071–1086.
40 <https://doi.org/10.1098/rstb.2007.2160>
- 41 Pontious, A., Kowalczyk, T., Englund, C., Hevner, R.F., 2008. Role of intermediate progenitor cells in
42 cerebral cortex development. *Dev. Neurosci.* 30, 24–32. <https://doi.org/10.1159/000109848>
- 43 Profant, O., Škoch, A., Balogová, Z., Tintěra, J., Hlinka, J., Syka, J., 2014. Diffusion tensor imaging
44 and MR morphometry of the central auditory pathway and auditory cortex in aging.
45 *Neuroscience* 260, 87–97. <https://doi.org/10.1016/j.neuroscience.2013.12.010>
- 46 Profant, O., Tintěra, J., Balogová, Z., Ibrahim, I., Jilek, M., Syka, J., 2015. Functional changes in the
47 human auditory cortex in ageing. *PloS One* 10, e0116692.
48 <https://doi.org/10.1371/journal.pone.0116692>
- 49 Rakic, P., 2007. The radial edifice of cortical architecture: from neuronal silhouettes to genetic
50 engineering. *BRR* 55, 204–219.
- 51 Rakic, P., 1995. A small step for the cell, a giant leap for mankind: a hypothesis of neocortical
52 expansion during evolution. *Trends Neurosci.* 18, 383–388.
- 53 Rakic, P., 1988. Specification of cerebral cortical areas. *Science* 241, 170–176.
- 54 Reuter, M., Rosas, H.D., Fischl, B., 2010. Highly accurate inverse consistent registration: a robust
55 approach. *NeuroImage* 53, 1181–1196.

- 1 Rigtters, S.C., Cremers, L.G.M., Ikram, M.A., van der Schroeff, M.P., de Groot, M., Roshchupkin,
2 G.V., Niessen, W.J.N., Baatenburg de Jong, R.J., Goedegebure, A., Vernooij, M.W., 2018.
3 White-matter microstructure and hearing acuity in older adults: a population-based cross-
4 sectional DTI study. *Neurobiol. Aging* 61, 124–131.
5 <https://doi.org/10.1016/j.neurobiolaging.2017.09.018>
- 6 Rosas, H.D., Liu, A.K., Hersch, S., Glessner, M., Ferrante, R.J., Salat, D.H., van der Kouwe, A.,
7 Jenkins, B.G., Dale, A.M., Fischl, B., 2002. Regional and progressive thinning of the cortical
8 ribbon in Huntington's disease. *Neurology* 58, 695–701.
- 9 Rosemann, S., Thiel, C.M., 2018. Audio-visual speech processing in age-related hearing loss: Stronger
10 integration and increased frontal lobe recruitment. *NeuroImage* 175, 425–437.
11 <https://doi.org/10.1016/j.neuroimage.2018.04.023>
- 12 Roth, T.N., Hanebuth, D., Probst, R., 2011. Prevalence of age-related hearing loss in Europe: a review.
13 *Eur. Arch. Oto-Rhino-Laryngol. Off. J. Eur. Fed. Oto-Rhino-Laryngol. Soc. EUFOS Affil.*
14 *Ger. Soc. Oto-Rhino-Laryngol. - Head Neck Surg.* 268, 1101–1107.
15 <https://doi.org/10.1007/s00405-011-1597-8>
- 16 Rufener, K.S., Oechslin, M.S., Wöstmann, M., Dellwo, V., Meyer, M., 2016. Age-Related Neural
17 Oscillation Patterns During the Processing of Temporally Manipulated Speech. *Brain Topogr.*
18 29, 440–458. <https://doi.org/10.1007/s10548-015-0464-0>
- 19 Salat, D.H., Buckner, R.L., Snyder, A.Z., Greve, D.N., Desikan, R.S.R., Busa, E., Morris, J.C., Dale,
20 A.M., Fischl, B., 2004. Thinning of the cerebral cortex in aging. *Cereb. Cortex* 14, 721–730.
21 <https://doi.org/10.1093/cercor/bhh032>
- 22 Ségonne, F., Dale, A.M., Busa, E., Glessner, M., Salat, D.H., Hahn, H.K., Fischl, B., 2004. A hybrid
23 approach to the skull stripping problem in MRI. *NeuroImage* 22, 1060–1075.
- 24 Shalom, D.B., Poeppel, D., 2008. Functional anatomic models of language: assembling the pieces.
25 *NST* 14, 119–127.
- 26 Steinhauer, K., Abada, S.H., Pauker, E., Itzhak, I., Baum, S.R., 2010. Prosody-syntax interactions in
27 aging: event-related potentials reveal dissociations between on-line and off-line measures.
28 *Neurosci. Lett.* 472, 133–138. <https://doi.org/10.1016/j.neulet.2010.01.072>
- 29 Thambisetty, M., Wan, J., Carass, A., An, Y., Prince, J.L., Resnick, S.M., 2010. Longitudinal changes
30 in cortical thickness associated with normal aging. *NeuroImage* 52, 1215–1223.
31 <https://doi.org/10.1016/j.neuroimage.2010.04.258>
- 32 Vannson, N., James, C., Fraysse, B., Strelnikov, K., Barone, P., Deguine, O., Marx, M., 2015. Quality
33 of life and auditory performance in adults with asymmetric hearing loss. *Audiol. Neurotol.*
34 20 Suppl 1, 38–43. <https://doi.org/10.1159/000380746>
- 35 Werkle-Bergner, M., Shing, Y.L., Müller, V., Li, S.-C., Lindenberger, U., 2009. EEG gamma-band
36 synchronization in visual coding from childhood to old age: Evidence from evoked power and
37 inter-trial phase locking. *Clin. Neurophysiol.* 120, 1291–1302.
38 <https://doi.org/10.1016/j.clinph.2009.04.012>
- 39 Wingfield, A., Lindfield, K.C., Goodglass, H., 2000. Effects of Age and Hearing Sensitivity on the
40 Use of Prosodic Information in Spoken Word Recognition. *J. Speech Lang. Hear. Res.* 43,
41 915. <https://doi.org/10.1044/jslhr.4304.915>
- 42 Wingfield, A., Wayland, S.C., Stine, E.A.L., 1992. Adult Age Differences in the Use of Prosody for
43 Syntactic Parsing and Recall of Spoken Sentences. *J. Gerontol.* 47, P350–P356.
44 <https://doi.org/10.1093/geronj/47.5.P350>
- 45 Wong, P.C.M., Ettlinger, M., Sheppard, J.P., Gunasekera, G.M., Dhar, S., 2010. Neuroanatomical
46 Characteristics and Speech Perception in Noise in Older Adults: *Ear Hear.* 31, 471–479.
- 47 Zatorre, R.J., Gandour, J.T., 2008. Neural specializations for speech and pitch: moving beyond the
48 dichotomy. *PBS* 363, 1087–1104.
- 49 Zekveld, A.A., Kramer, S.E., Festen, J.M., 2011. Cognitive Load During Speech Perception in Noise:
50 The Influence of Age, Hearing Loss, and Cognition on the Pupil Response. *Ear Hear.* 32, 498.
51 <https://doi.org/10.1097/AUD.0b013e31820512bb>

Table Descriptions

Table 1:

This table shows the pitch of each syllable of the three versions of the word /Hubschrauber/ used for the mismatch negativity experiment. In addition, in the bottom, the predictions about the occurrence of the mismatch negativity (MMN) based on these pitch differences are described.

Table 2:

Table 2 shows the peak amplitudes and their respective latencies for each syllable and for each stimulus (Standard, Deviant 1, Deviant 2) and each age group (YA, OA) separately. Standard deviations are shown in brackets.

Table 3:

This table shows the mean (M) and standard deviation (SD) of cortical thickness (CT) in mm and mean cortical surface area (CSA) in mm² of all six bilateral ROIs for younger (YA) and older adults (OA) separately. Furthermore, F values for statistical comparison of CT and GMV between YA and OA are described.

Figure Legends*Figure 1:*

This Figure shows the bilateral pure-tone thresholds separately for the younger (YA) (N=15) and the older adults (OA) (N=23). Both groups can be considered as normal hearing, even though the pure-tone average differs.

Figure 2:

Figure 2 depicts the spectrogram of the three stimuli consisting of the German word /Hubschrauber/ with three different word stress patterns used for the mismatch negativity experiment. On the top, the standard stimulus is shown with a stress on the first syllable. In the middle, the Deviant 1 with a stress on the second syllable is depicted, while on the bottom the Deviant 2 with a stress on the third syllable is shown. The left axis represents the scaling for the stimulus spectrum, while the right axis (in blue) shows the f_0 contour indicating the different stress patterns of the three stimulus versions.

Figure 3:

Figure 3 shows the averaged ERP time-locked to word onset at electrode Cz, separately for each stimulus (dark = Standard, light = Deviant 1, very light = Deviant 2) and age group. Time-locked to the onset of each syllable, there are MMNs occurring after approximately 200 ms. Peak amplitudes were analyzed statistically time-locked to each syllable.

Figure 4:

This Figure shows the peak amplitude differences between the deviants and the standard stimuli for each deviant condition separately for the time-locked signal to each of the three Syllable onsets. Dark grey indicates YA (N=15), light grey OA (N=23). *= $p < .05$ and ***= $p < .001$ indicating significant difference between deviant and standard peak amplitude implying a significant occurrence of an MMN. The dashed lined boxes point to the conditions in which we expected a significant MMN to occur.

Figure 5:

This Figure shows the accuracy for the word stress discrimination task when the word stress was different in 20, 30, or 40 Hz as well as when it was on the first, second, or third syllable of the word /Hubschrauber/. Dark grey indicates YA (N=14), light grey OA (N=19).

Figure 6:

Figure 6 depicts the significant correlations between brain structure and mismatch negativities (MMN) for the older adults (N=23). Older individuals who had larger surface area in the left Heschl's sulcus and in the left supratemporal gyrus (STG) also evoked larger MMN magnitudes.

	Syllable 1	Syllable 2	Syllable 3
Standard stimulus	238.53 Hz	173.91 Hz	169.67 Hz
Deviant 1	220.48 Hz	246.91 Hz	169.67 Hz
Deviant 2	220.48 Hz	173.91 Hz	223.21 Hz
Hypotheses	Time-locked to Syllable 1, a MMN should occur in both deviants (difference: 18.05 Hz)	Time-locked to Syllable 2, a MMN should only occur in Deviant 1 (difference: 73 Hz)	Time-locked to Syllable 3, a MMN should only occur in Deviant 2 (difference: 53.54 Hz)

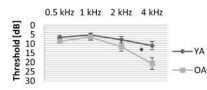
Peak amplitudes in μV						
	Syllable 1		Syllable 2		Syllable 3	
	YA	OA	YA	OA	YA	OA
Standard	-1.14 (.75)	-.52 (.63)	-2.11 (1.13)	-1.50 (.75)	-.98 (.58)	-.90 (.60)
Deviant 1	-1.32 (1.06)	-.81 (.90)	-2.54 (1.41)	-2.06 (1.08)	-1.08 (1.22)	-.77 (1.09)
Deviant 2	-1.52 (1.23)	-.63 (.84)	-2.70 (1.71)	-1.77 (1.09)	-1.26 (1.02)	-1.29 (1.06)

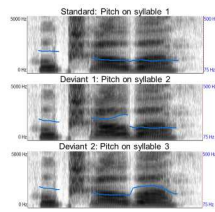
Latencies of peak in ms						
	Syllable 1		Syllable 2		Syllable 3	
	YA	OA	YA	OA	YA	OA
Standard	312.50 (37.77)	323.54 (12.06)	165.36 (22.88)	179.69 (52.18)	189.58 (46.90)	212.21 (33.87)
Deviant 1	319.01 (35.84)	325.32 (26.69)	172.27 (35.69)	187.16 (54.35)	210.03 (59.91)	210.34 (41.92)
Deviant 2	334.64 (30.08)	330.84 (24.77)	179.69 (35.53)	196.76 (52.40)	196.88 (40.11)	191.07 (34.04)

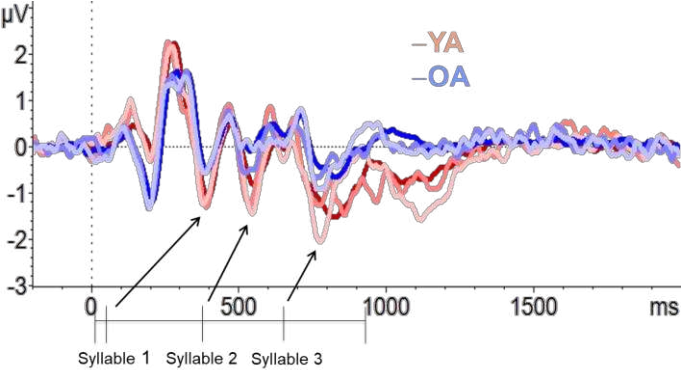
	CT					
	YA			OA		
	M	SD	M	SD	F	p
l PT	2.65	.15	2.43	.12	$F(1,34)=18.92$	<.001 ***
l PP	3.58	.23	3.29	.29	$F(1,34)=9.53$.004 *
l STG	3.08	.16	2.85	.16	$F(1,34)=18.54$	<.001 ***
l STS	2.52	.13	2.23	.11	$F(1,34)=50.12$	<.001 ***
l HS	2.62	.37	2.12	.35	$F(1,34)=10.75$.002 *
l HG	2.59	.18	2.19	.22	$F(1,34)=24.75$	<.001 ***
r PT	2.61	.17	2.36	.16	$F(1,34)=18.80$	<.001 ***
r PP	3.63	.21	3.24	.30	$F(1,34)=18.39$	<.001 ***
r STG	3.19	.11	2.87	.17	$F(1,34)=33.01$	<.001 ***
r STS	2.55	.11	2.33	.14	$F(1,34)=21.33$	<.001 ***
r HS	2.87	.28	2.34	.25	$F(1,34)=32.68$	<.001 ***
r HG	2.62	.21	2.25	.24	$F(1,34)=16.60$	<.001 ***

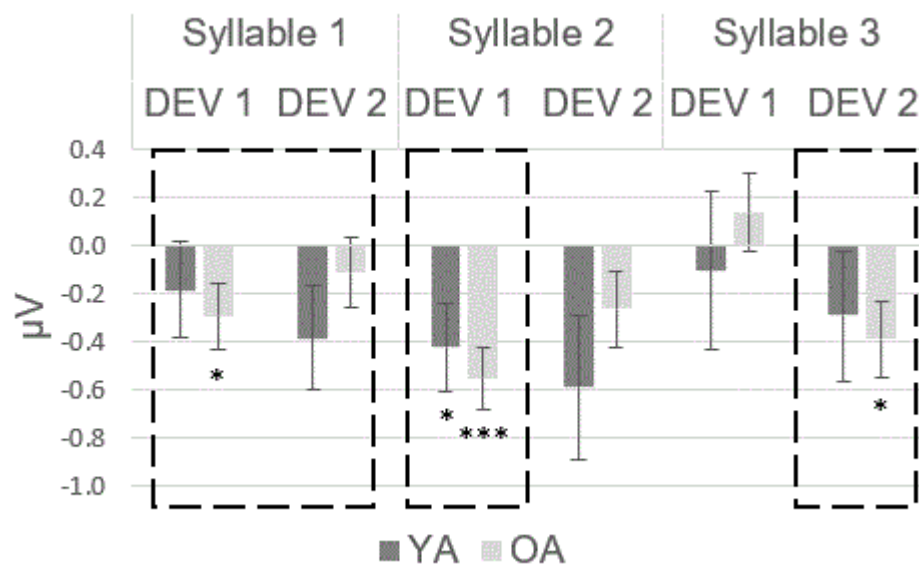
	CSA					
	YA			OA		
	M	SD	M	SD	F	p
l PT	785.37	132.30	692.07	104.73	$F(1,34)=11.71$.002 *
l PP	458.93	60.43	416.83	50.95	$F(1,34)=7.38$.010
l STG	1852.20	170.33	1802.28	168.66	$F(1,34)=.48$.490
l STS	3268.43	481.65	3185.61	427.26	$F(1,34)=.35$.557
l HS	239.63	27.25	241.57	37.45	$F(1,34)=.02$.903
l HG	434.90	90.93	371.85	54.75	$F(1,34)=9.09$.005
r PT	550.23	82.77	518.04	62.10	$F(1,34)=4.11$.050
r PP	457.30	63.03	433.37	58.65	$F(1,34)=2.38$.132
r STG	1597.57	152.00	1557.07	161.25	$F(1,34)=.55$.464
r STS	3975.37	392.90	3795.76	421.50	$F(1,34)=2.23$.144
r HS	202.20	26.40	206.70	27.56	$F(1,34)=.03$.869
r HG	310.80	49.90	273.50	40.64	$F(1,34)=9.41$.004 *

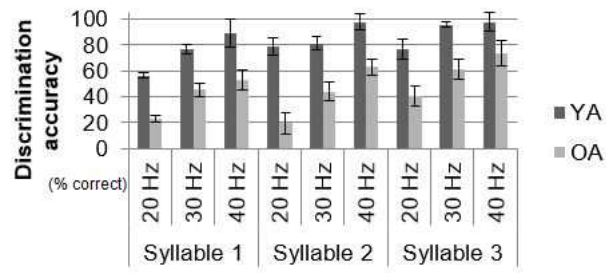
Note: $p<.05$ trend, $*p<.0042$, Bonferroni corrected, $***p<.001$

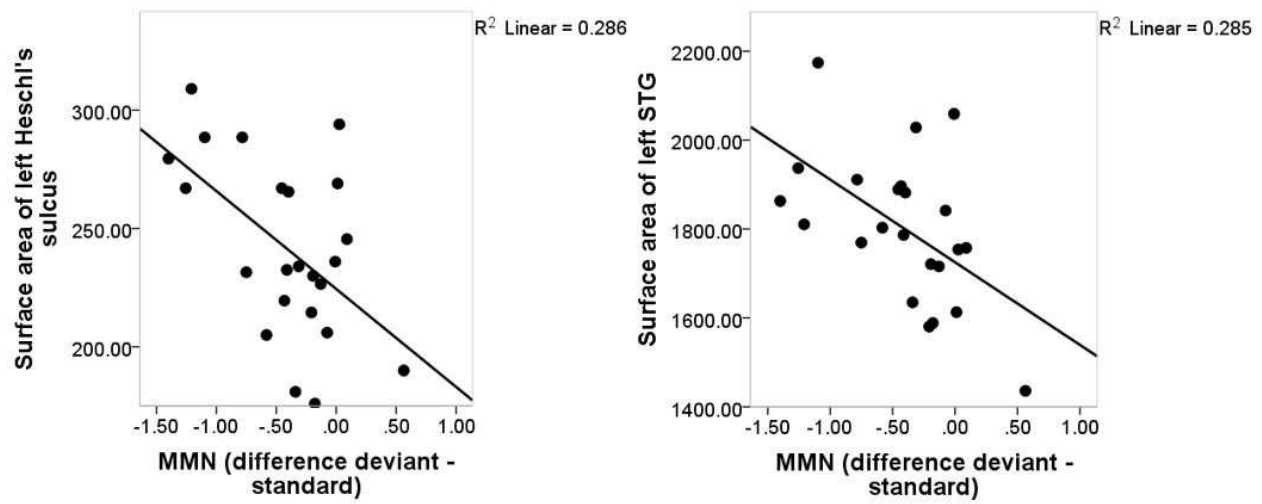












Highlights

- Mismatch negativity (MMN) patterns reveal higher neural sensitivity to words stress in older than younger adults
- Greater cortical thickness in a right auditory-related area is related to better performance in pitch discrimination in older adults
- Larger cortical surface area in left auditory-related areas is associated with higher MMN magnitude evoked by word stress in older adults

In the name of all authors of this manuscript, I confirm that all authors have reviewed the contents of the manuscript being submitted, approved of its contents and validated the accuracy of the data. There is no conflict of interests to declare.

A handwritten signature in blue ink, appearing to read 'N. Giroud', on a light yellow background.

Dr. Nathalie Giroud